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PHYLOGEOGRAPHY OF THE TIDEWATER GOBY, *EUCYCLOGOBIUS NEWBERRYI* (TELEOSTEI, GOBIIDAE), IN COASTAL CALIFORNIA

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Abstract.—The tidewater goby, *Eucyclogobius newberryi,* inhabits discrete, seasonally closed estuaries and lagoons along approximately 1500 km of California coastline. This species is euryhaline but has no explicit marine stage, yet population extirpation and recolonization data suggest tidewater gobies disperse intermittently via the sea. Analyses of mitochondrial control region and cytochrome *b* sequences demonstrate a deep evolutionary bifurcation in the vicinity of Los Angeles that separates southern California populations from all more northerly populations. Shallower phylogeographic breaks, in the vicinities of Seacliff, Point Buchon, Big Sur, and Point Arena segregate the northerly populations into five groups in three geographic clusters: the Point Conception and Ventura groups between Los Angeles and Point Buchon, a lone Estero Bay group from central California, and San Francisco and Cape Mendocino groups from northern California. The phylogenetic relationships between and patterns of molecular diversity within the six groups are consistent with repeated, and sometimes rapid, northward and southward range expansions out of central California caused by Quaternary climate change. Plio-Pleistocene tectonism, Quaternary coastal geography and hydrography, and historical human activities probably also influenced the modern geographic and genetic structure of *E. newberryi.* The phylogeography of *E. newberryi* is concordant with phylogeographic patterns in several other coastal California taxa, suggesting common extrinsic factors have had similar effects on different species. However, there is no evidence of a phylogeographic break coincident with a biogeographic boundary at Point Conception.

Key words.—AMOVA, biogeography, mitochondrial DNA, phylogeography, Pleistocene, Pliocene, Point Conception.

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In the southeastern United States intraspecific phylogenies of coastal maritime animals often are concordant with traditionally recognized zoogeographic patterns. Mitochondrial DNA (mtDNA) analyses of black sea bass, seaside sparrow, horseshoe crab, American oyster, diamondback terrapin, and toadfish reveal close geographic concordance between intraspecific phylogenetic gaps and the Carolina-Caribbean zoogeographic provincial boundary, near Cape Canaveral (Briggs 1974; Avise 1992). The concordance of these patterns suggests that intraspecific monophyletic groups distinguished by large phylogenetic gaps arise from long-term zoogeographic barriers to gene flow (Avise et al. 1987). That is, historically established barriers to the movement of animals generated by circulation patterns, temperature regimes, and coastal topography similarly influence both intraspecific and interspecific patterns of diversity.

In the southwestern United States, however, intraspecific phylogenies of coastal maritime animals apparently are not concordant with zoogeographic patterns (Burton 1998). Discordance has been documented at two levels. First, despite a well-recognized biogeographic boundary at Point Conception (Briggs 1974; Doyle 1985), which is marked by strong discontinuities in temperature, hydrography, salinity, dissolved oxygen, and topography (Briggs 1974; Seapy and Littler 1980; Browne 1994), most coastal marine taxa studied have weak or no intraspecific phylogeographic structure (Murphy 1978; Mastro et al. 1981; Ford and Mitton 1993; Sarver and Foltz 1993; Van Syoc 1994; Palumbi 1995; Beauchamp and Powers 1996; Edmands et al. 1996; Hellberg 1996; see summary in Burton 1998). Second, in the few coastal marine taxa that do have deep intraspecific phylogeographic structure, the principal phylogenetic gaps lie tens to hundreds of kilometers south of the biogeographic break at Point Conception (Burton 1998; Marko 1998; Bernardi 2000). Thus, there appear to be important differences between phylogeographic and biogeographic processes in the southeastern and southwestern United States.

Burton (1998) suggested the discrepancy between southeastern and southwestern phylogeographic studies might be attributable to three factors. First, southwestern studies predominantly used molecular markers of lower resolution (allozymes) than those used in southeastern studies (mtDNA). Second, in contrast to Cape Canaveral, Point Conception separates faunas that are not closely related. Therefore, unlike patterns across Cape Canaveral, there is no reason to expect phylogeographic and biogeographic patterns to be concordant across Point Conception. Third, the geological processes that contributed to concordant patterns in the Southeast were unique to that region and were unimportant in the Southwest.

MtDNA markers since have proven informative in the Southwest, but they have not resolved the discrepancy between southeastern and southwestern studies (Burton 1998; Marko 1998; Bernardi 2000). Phylogeographic gaps still are discordant with a biogeographic break at Point Conception. Thus, having eliminated low-resolution molecular markers as the source of disagreement, the discordance may be attributable to different biogeographic or geological processes in the Southeast and Southwest.

The extrinsic processes that affect phylogeographic patterns are studied most easily in animals of low-dispersal abil-

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ity. In contrast to high-dispersal species, in which geneflow often precludes genetic subdivision (e.g., Waples 1987; Palumbi 1995; Lessios et al. 1998), and intermediate-dispersal species, which must be sampled extensively (Waples 1998; Dawson 2000), low-dispersal species often are composed of genetically and geographically highly structured populations (e.g., Burton 1998; Bernardi 2000). Thus, low-dispersal species provide many opportunities to compare the depths and positions of intraspecific phylogeographic breaks with the magnitude and locations of extrinsic factors (e.g., Burton 1998; Bernardi 2000).

The tidewater goby, *Eucyclogobius newberryi,* is well suited to a study of extrinsic processes that affect the phylogeography of coastal southwestern taxa for several reasons. First, its wholly estuarine life history suggests extremely low dispersal. Eggs are brooded in burrows, a larval stage (which lasts a few days) is completed amid estuarine vegetation, and juveniles and adults are benthic. Moreover, reproduction occurs primarily between late spring and early autumn, when *E. newberryi* habitat often is isolated from the ocean by wave-built berms (Swift et al. 1989; Smith 1990; Capelli 1997; Ballard et al. 1999; Swenson 1999). Second, however, while *E. newberryi* lacks an explicit marine phase (Swift et al. 1989), there has been at least one record of a tidewater goby from coastal waters since 1923 (Ichthyology Collection no. CAS31769, Museum of Natural History, California Academy of Sciences, San Francisco, CA) and tidewater gobies must disperse, at least occasionally, via coastal waters during bouts of extirpation and recolonization (Lafferty et al. 1999a,b). Third, its range, from the Smith River in northern California to the Santa Margarita River in southern California (Miller and Lea 1972; Swift et al. 1989; but see Crabtree 1985; Fig. 1), encompasses at least one well-recognized ''provincial'' zoogeographic boundary (Briggs 1974; Horn and Allen 1978; Seapy and Littler 1980), several less severe biogeographic boundaries (Horn and Allen 1978; Seapy and Littler 1980), and a number of phylogeographic boundaries of differing severity (Burton 1998; Bernardi 2000). Concomitantly, historical records suggest that the range of *E. newberryi* is fragmented by coastal topography and the distribution of habitat (Swift et al. 1989). Fourth, *E. newberryi* is composed of a linear array of discrete populations, which allows empirical patterns of gene flow to be interpreted in light of the theoretical expectations of the stepping-stone model (Kimura and Weiss 1964; Slatkin and Maddison 1990; Hellberg 1995; Vrijenhoek 1997). Finally, *E. newberryi* has several corollaries with southeastern taxa that exhibit deep phylogeographic structure (e.g., it is estuarine, a vertebrate, and has limited dispersal ability) that facilitate comparisons between species and between regions.

Here, we describe the phylogeography and probable evolutionary history of *E. newberryi,* using mtDNA sequence data. Variation in both mitochondrial control region (mtCR) and cytochrome apoenzyme *b* (cyt *b*) sequences is high and geographically structured. These data suggest a Plio-Pleistocene origin of the diversity now observed in *E. newberryi* and at least two episodes of evolution driven by Quaternary climate change. The modern phylogeographic structure of *E. newberryi* probably also has been influenced by tectonism, sea-level change, coastal hydrography and geography, and natural and anthropogenic extirpations. Notably, the phylogeography of *E. newberryi* is similar to the phylogeographies of *Tigriopus californicus* (Burton 1998) and *Embiotoca jacksoni* (Bernardi 2000), suggesting shared extrinsic factors have had similar effects among species. Importantly, there is no evidence of a phylogeographic break coincident with the biogeographic boundary at Point Conception.

Materials and Methods

Collections

Eucyclogobius newberryi individuals were collected from 31 locations between 1990 and 1999 (Fig. 1; Table 1). Specimens were caught in seine nets, individually marked, and stored at −80°C. Arrow gobies, *Clevelandia ios,* the putative sister taxon of the tidewater goby (M. N Dawson and D. K. Jacobs, unpubl. data), were collected from Long Beach, California, during 1997, preserved in 70% ethanol, and stored at −20°C.

DNA Extraction, Polymerase Chain Reaction, and Sequencing

Total DNA was extracted from muscle using a CTAB extraction protocol modified from Dawson et al. (1998). Polymerase chain reactions (PCRs) using *Taq* polymerase (Perkin Elmer, Boston, MA), and MJ Research (Waltham, MA) MiniCyclers, began with a 5-min denaturation step, followed by 32 cycles, each consisting of 45 sec at 94°C, 45 sec at 49–51°C, and 60–90 sec at 72°C, depending on both the template and primers. PCRs terminated with a 10-min extension step (72°C), then refrigeration (4°C). Creatine kinase intron 6 was amplified using primers CK6-5′ and CK7-3′ (Palumbi et al. 1991), mtCR using primers CR-A and CR-M (Lee et al. 1995), and cyt *b* using EnCytB-for (5′-CCTTAGTAGACCTCCCCGCACCC-3′) and EnCytB-rev (5′-CCCCAGATYCACTGAMCRAGGG-3′).

Secondary structure in amplified mtCR inhibited direct sequencing. This problem was resolved reliably only by cloning (TOPO TA cloning kit from Invitrogen, Carlsbad, CA; Flexiprep kit from Pharmacia, Piscataway, NJ) PCR fragments prior to sequencing on Applied Biosystems (Foster City, CA) 373 Autosequencers. Invitrogen's M13Reverse and M13Forward primers and four internal mtCR primers (Dawson 2000) were used in sequencing.

PCR and sequencing error.—PCR error rate was assessed by repeating the amplification, cloning, and sequencing of mtCR from 10 Southern specimens (see Results). Overall, 12 identifiable PCR errors in 8608 bases of repeat sequence, implied a detectable PCR error rate of one in 717 bases. Sequencing of 98 mtCR sequences with $\geq$ 2 primers generated usually up to several hundred bases of matching sequence, indicating sequencing error was rare.

Sequence and Phylogenetic Analyses

The identities of sequences were confirmed by BLAST searching GenBank (Altschul et al. 1997) and by comparison to published sequences (e.g., Lee et al. 1995) before alignment in ClustalW (Thompson et al. 1994) and by eye. Cyt *b* and creatine kinase exon sequences were validated by trans-

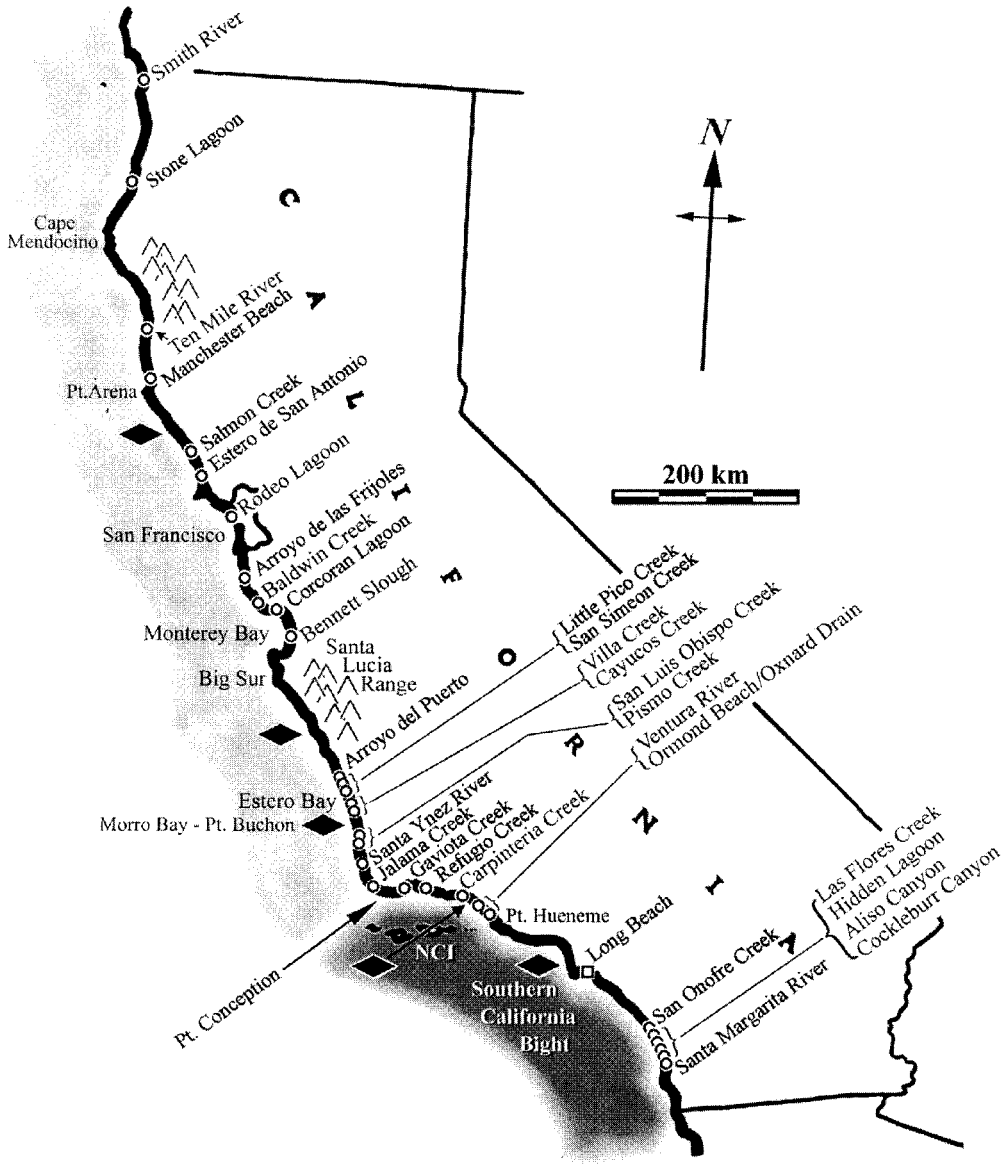

FIG. 1. Schematic map of California showing the sample locations of *Eucyclogobius newberryi* (circles) and the outgroup *Clevelandia ios* (square) and the principal features mentioned in the text. Light shading indicates the Oregonian Province and dark shading the Californian Province, whose boundaries meet near Point Conception (Doyle 1985), the approximate center of the several-hundred-kilometer long California Transition Zone (Seapy and Littler 1980). Except the northern channel islands (NCI; from west to east: San Miguel, Santa Rosa, Santa Cruz, and Anacapa Islands), the California Channel Islands are not shown. The Palos Verdes Peninsula lies immediately west of Long Beach. The Los Angeles Region (LAR) spans 50–100 km north and south of Long Beach. Black diamonds indicate the regions in which phylogeographic breaks were found in *E. newberryi* (this study).

lation into amino acid data using DNA Strider 1.2 (C. Marck, Service de Biochimie et de Génétique Molécularie, Direction des Sciences de la Vie, CEA, France).

Haplotype diversity, nucleotide diversity, genetic distances, and mismatch distributions were calculated using haplotypes inferred from a distance matrix constructed by Arlequin version 1.1 (Schneider et al. 1997). Mean base composition, and the ratios of variable : constant, transitions : transvertions, and polymorphic cyt *b* first : second : third positions were calculated for mtCR and cyt *b* using Arlequin version 1.1. The sequence data were tested for phylogenetic structure using the permutation tail probability test (PTP; Faith and Cranston 1991) in PAUP 4.0b3a (Swofford 2000) and the sequence data statistics used to choose appropriate weighting schemes for phylogenetic analyses.

Phylogenetic analyses used combined mtCR and cyt *b* data because these sequences are linked closely on the predominantly nonrecombining mitochondrial genome (Brown 1985) and their properties, as calculated above, were very similar (see Results). Weighting schemes varied from unweighted to those that reflected and exceeded the relative frequencies of transitions, transversions, and variable positions in mtCR, cyt *b*, and first, second, and third positions of cyt *b*. Gaps were both included in and excluded from analyses because

TABLE 1. List of collection localities and sample sizes (north to south). Two of the 31 collection localities, Santa Ynez river and Las Flores Creek, were visited twice, first in 1990 and second in 1998. One sequence from each site marked with an asterisk was not used in maximum-likelihood analyses due to missing data. Creatine kinase intron 6 also was sequenced from one fish from each site marked with two asterisks.

County	Site	No. of samples
Del Norte (DN)	Smith River	3
Humbolt (H)	Stone Lagoon**	3
Mendocino (Me)	Ten Mile River	2
	Manchester State beach**	3
Sonoma (So)	Salmon Creek	2
Marin (Ma)	Ester de San Antonio	4
	Rodeo Lagoon*	3
San Mateo (SM)	Arroyo de las Frijoles**	4
Santa Cruz (SC)	Baldwin Creek	2
	Corcoran Lagoon	2
Monterey (M)	Bennett Slough*	3
San Luis Obispo (SLO)	Arroyo del Puerto	3
	Little Pico Creek	3
	San Simeon Creek	2
	Villa Creek	1
	Cayucos Creek*	2
	San Luis Obispo Creek	2
	Pismo Creek	3
Santa Barbara (SB)	Santa Ynez River A**	4
	Santa Ynez River B	2
	Jalama Creek	2
	Gaviota Creek	2
	Refugio Creek**	4
	Carpinteria Creek	3
Ventura (V)	Ventura River	4
	Ormond Beach	3
San Diego (SD)	San Onofre Creek**	3
	Las Flores Creek A	3
	Las Flores Creek B	2
	Hidden Lagoon	2
	Aliso Canyon	2
	Cockleburr Canyon	1
	Santa Margarita River**	4

their utility may vary between datasets (e.g., Swofford et al. 1996; van Dijk et al. 1999). Maximum-likelihood (ML) analyses of the complete dataset (except three taxa and occasional positions with missing data; Table 1) used the default options of PUZZLE 4.0.2 (Strimmer and von Haeseler 1996, 1999) and 5000 puzzling steps; transitions and transversions were weighted according to their frequencies in the dataset. ML analyses also were completed in PAUP 4.0b3a using the default options and 2000 puzzling steps. In addition, weighted and unweighted maximum-parsimony (MP) searches and bootstrap analyses were completed in PAUP 4.0b3a, and decay analyses calculated using TreeRot (Sorenson 1996) and PAUP 3.1.1 (Swofford 1993). UPGMA and neighbor-joining (NJ) trees were constructed from Jukes and Cantor, Kimura two-parameter, and Jin and Nei corrected genetic distances in PHYLIP 3.573c (Felsenstein 1995). *Clevelandia ios* subsequently was included in ML analyses to root the *E. newberryi* tree.

The geographic structure of genetic variation was assessed using analysis of molecular variation (AMOVA; Excoffier et al. 1992) in Arlequin 1.1 for Windows 95 (Schneider et al. 1997) by defining phylogeographic groups in accordance with the results of phylogenetic analyses. After testing the phylogeographic structure in its entirety, each phylogeographic group was collapsed, in turn, to examine the relative contributions of different phylogeographic breaks to overall phylogeographic structure. The relative contributions of phylogeographic breaks to hierarchical genetic structure also were investigated by comparing mean pairwise genetic and geographic distances between northern and southern members of all phylogeographic groups. Central members also were recognized, distinct from northern and southern members, in geographically larger groups that were well sampled to prevent averaging over very large geographic distances. First, the Mantel test (10,000 permutations) was used to test for correlation between mean pairwise sequence and geographic distances separating northern, southern, and central members of all phylogeographic groups (R Package 4.0; Casgrain and Legendre 1999). The Mantel test also was used to test for significantly different amounts of genetic variation at the levels of intragroup, intergroup, and across the Los Angeles region by permuting the genetic distance matrix against model binary matrices (Casgrain and Legendre 1999; Lemaire et al. 2000). Subsequently, pairwise genetic differences were related to mean pairwise geographic distances using ordinary least-squares regression (Hellberg 1994) and the regressions compared using analysis of covariance (ANCOVA) in SYSTAT 6.0 for Windows 3.1.

RESULTS

Sequence Analyses

Creatine kinase, intron 6.—A total of 440 nucleotides, including the entire sixth intron and 69 bases of flanking coding region, were amplified from seven tidewater gobies (Table 1). Only two positions were variable, and neither was parsimony informative nor differentiable from PCR error. These sequences are not discussed further.

MtCR and cyt b.—A total of 1293 bases of mtDNA, in two fragments, were sequenced from 88 *E. newberryi* (Fig. 1, Table 1). One fragment (890 nucleotides long) contained almost the entire mtCR plus 16 bases from the 3′ end of tRNA-proline. The mean percent base composition of this fragment was 16.5G:32.9A:31.0T:19.5C. It contained 109 variable positions: 72 transitions, 35 transversions, and seven indels. There were 65 unique haplotypes. A second fragment (403 nucleotides long) from the 5′ portion of cyt *b* had a mean percent base composition 20.8G:19.1A:33.9T:26.2C. There were 53 variable positions: 43 transitions and 14 transversions. Fifteen first, nine second, and 29 third codon positions were variable, resulting in 22 amino acid substitutions of which six were parsimony informative. There were 38 unique haplotypes. Pairwise sequence differences of both mtCR (range: 0–4.71%, modes: 1.12%, 3.81%) and cyt *b* (range: 0–4.71%, modes: 0.99%, 3.72%; Fig. 2) were distributed bimodally.

The transition : transversion ratio calculated by PUZZLE 4.0.2 for combined mtCR and cyt *b*, no missing data, was 2.95 ± 0.41 (mean ± SE). Nucleotide diversity ($\pi \pm$ SD) was 0.0203 ± 0.0100 and haplotype diversity ($h \pm$ SD) was 0.9893 ± 0.0054. An adjusted estimate, and probably a slight underestimate, of molecular diversity was calculated by ex-

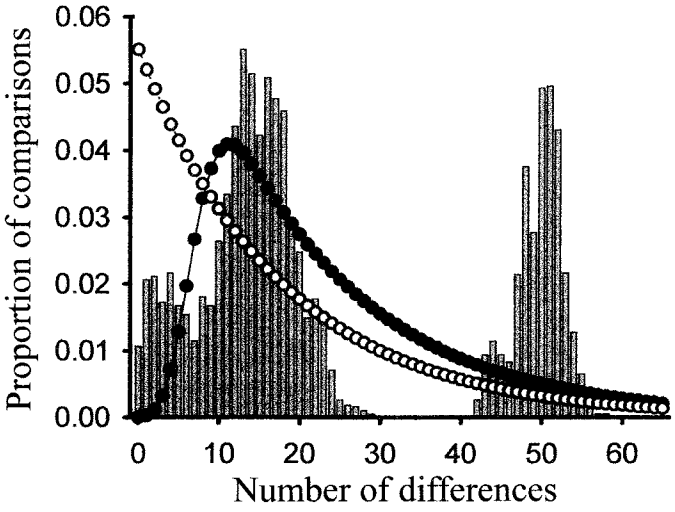

FIG. 2. Mismatch distribution constructed using uncorrected pairwise differences in combined mtCR and cyt *b* sequences of 88 *Eucyclogobius newberryi*, (Θ_0 = 17.14, τ = 7.48, Harpending's raggedness index [HRI] = 0.003). The observed bimodal distribution (bars) shows two distinct population segments within *E. newberryi* and differs significantly from the expected distributions of pairwise distances in populations that experienced long-term stable size (white circles, dashed line; $\chi^2 = 6733$, df = 58, $P < 0.005$) or historically rapid expansion (black circles, solid line; $\chi^2 = 25735$, df = 58, $P < 0.005$).

cluding all 70 autapomorphic characters (i.e., potential PCR error) from the sequence data. The adjusted nucleotide diversity ($a\pi$) was 0.0190 ± 0.0093 and adjusted haplotype diversity (ah) was 0.9660 ± 0.0104.

Phylogenetic Reconstructions

PTP analyses indicated high support for phylogenetic structure in the data (50 permutations, $P = 0.02$). ML, MP, and distance analyses of combined mtCR and cyt *b* all recovered trees in which the major topology was very similar (Fig. 3; Dawson 2000). Two genetically and geographically divergent clades, Southern and Northern, were recovered unambiguously by all analyses. The Southern clade was represented solely by a monophyletic San Diego County group. The Northern clade, in contrast, comprised five groups in three geographic clusters: the Point Conception and Ventura groups from north of Los Angeles but south of Point Buchon, a lone Estero Bay group from central California, and San Francisco and Cape Mendocino groups from northern California. All groups except San Francisco were reciprocally monophyletic in at least one suite of phylogenetic analyses (ML, MP, or distance). Other analyses, however, reduced the monophyletic status of Estero Bay and Point Conception to paraphyly, with respect to all other Northern groups and the Ventura group, respectively. The status of the San Francisco group, which usually was paraphyletic with respect to Cape Mendocino (Fig. 3), was reduced in some analyses to polyphyly. Although there generally was little phylogeographic structure within the six major groups, there was some support for several small subgroups, including, a monophyletic clade in Arroyo de las Frijoles, distinct northern and southern Estero Bay haplotypes, and several hierarchical subgroups in the Cape Mendocino clade, with more derived haplotypes generally occurring further north.

Geographic Structure

AMOVA of sequence data partitioned into the San Diego, Ventura, Point Conception, Estero Bay, San Francisco, and Cape Mendocino groups confirmed that considerable genetic variation in *E. newberryi* (Table 2) was hierarchically geographically structured. Genetic diversity in *E. newberryi* was significant within populations, among populations within regions, and among regions (AMOVA, $P < 0.001$ at all levels; Table 3, note 1). Collapsing each clade in turn indicated that the significant regional structure was contributed to by all groups but was attributable principally to a phylogeographic break between Southern and Northern clades in the Los Angeles region (LAR; Table 3, notes 2–6). Per unit geographic distance, however, a phylogeographic boundary in the vicinity of Point Buchon and Morro Bay was equally severe (MB/PtB; Table 4).

The predominant effect of LAR on phylogeographic structure also was apparent in regressions of genetic distance on geographic distance (Fig. 4). Pairwise genetic differences across LAR significantly exceeded differences across all other phylogeographic breaks ($F_{1,10} = 33.8$, $P < 0.001$). In turn, pairwise genetic differences between Northern groups (i.e., across the lesser phylogeographic breaks) were significantly greater than pairwise genetic differences within groups ($F_{1,10} = 3423$, $P < 0.001$; Fig. 4). These three levels of dissimilarity also were supported by permutations of the pairwise genetic distance matrix against model matrices (LAR vs. other breaks, Mantel's $r = 0.9759$, $P = 0.013$; intergroup vs. intragroup distances, Mantel's $r = -0.6871$, $P < 0.001$). Considering only comparisons between phylogeographic groups within the Northern clade, there was a significant positive correlation between mean genetic distance and mean geographic distance (Mantel's $r = 0.4418$, $P = 0.018$; Fig. 4). However, the relationship between migration rate and geographic distance was weak ($\log[Nm] = 0.8 - 0.744 \log[\text{km}]$, $R^2 = 0.251$, $P < 0.001$).

The six phylogeographic groups indicated by phylogenetic analyses and AMOVA also were distinct in their patterns of genetic diversity (Fig. 5, Table 5). Estero Bay and San Francisco groups were the most diverse. Their greatest pairwise sequence differences being about twice the greatest differences observed in more southerly groups and in the Cape Mendocino group. The Estero Bay and San Francisco groups, as well as Cape Mendocino, also had more ragged mismatch distributions than groups south of Estero Bay. The mismatch distributions of the three most northerly groups, which may be polymodal, differed significantly from the smooth distributions expected to result from historical sudden population expansion (Fig. 5A–C; Rogers and Harpending 1992). In contrast, the mismatch distribution of the Point Conception clade was smooth, unimodal, and conformed closely to the model of sudden expansion (Fig. 5D), whereas the skewed, highly leptokurtic distribution of pairwise differences in the San Diego clade suggested a recent bottleneck (Fig. 5F; Rogers and Harpending 1992). The Ventura group did not conform to the sudden expansion model (Fig. 5E) because it was poor-

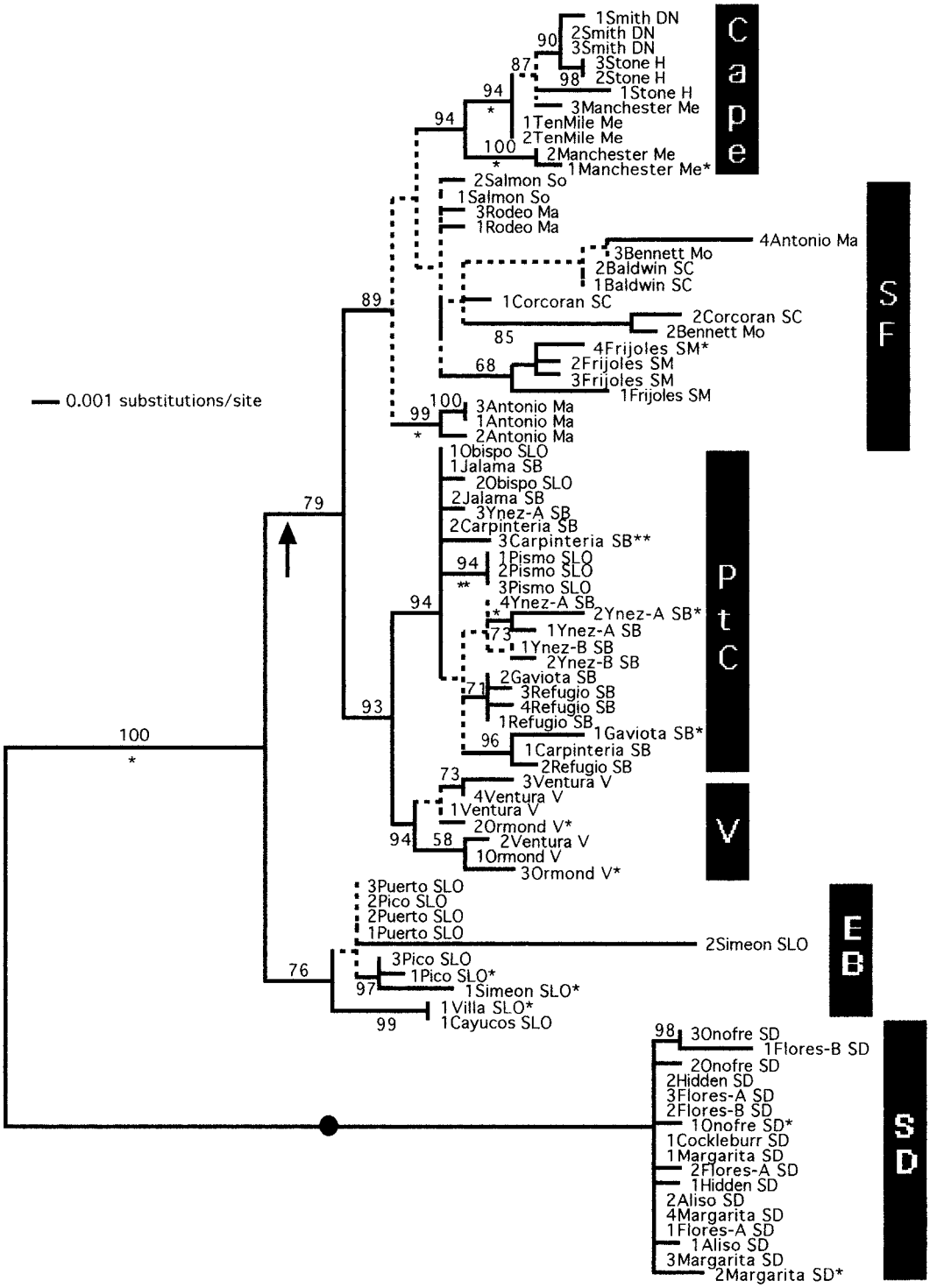

FIG. 3. Maximum likelihood (ML) phylogeny calculated in PAUP 4.0b3a overlayed with the ML phylogeny calculated in PUZZLE 4.0.2 (log L = −2880; unconstrained = −2248). Branches that appear in the PAUP tree but not in the PUZZLE tree are dashed (i.e., reducing these branches to polytomies yields the most resolved tree consistent with both PAUP and PUZZLE analyses). Numbers above branches indicate percent support calculated in PUZZLE. Each asterisk below a branch indicates one synapomorphic amino acid substitution; asterisks at the tips of branches indicate autapomorphic amino acid substitutions. The black circle shows the root of the tree, as determined by ML analyses of the *Eucyclogobius newberryi* dataset appended with mtCR and cyt *b* sequence data from *Clevelandia ios.* The arrow shows the alternative placement of 2SimeonSLO indicated by maximum-parsimony analyses (Dawson 2000). This alternative basal placement is attributable to the absence from 2SimeonSLO of (1) most synapomorphies that unite all other Estero Bay sequences (thus its long branch length in this figure); and (2) synapomorphies that distinguish groups within other Northern groups; that is, 2SimeonSLO contains characters that generally are symplesiomorphic or autapomorphic relative to other northern sequences. The three sequences excluded from ML analyses (see footnote to Table 1) were closely related to others from the same sites in parsimony analyses (Dawson 2000).

TABLE 2. Mean genetic distances within and between phylogeographic groups of *Eucyclogobius newberryi*. Groups are labeled as in Figure 3. Above diagonal, average number of pairwise differences between populations; diagonal elements, average number of pairwise differences within a population; below diagonal, corrected average pairwise difference. Distance method: Kimura two-parameter, calculated in Arlequin version 1.1.

	Cape	SF	EB	PtC	V	SD
Cape	4.573	11.349	18.283	15.024	14.806	50.461
SF	4.441	9.244	17.016	14.694	14.325	50.461
EB	12.952	9.349	6.090	12.990	13.404	45.411
PtC	10.747	8.082	7.955	3.981	7.415	49.680
V	10.747	7.930	8.586	3.652	3.546	46.655
SD	47.416	45.080	41.607	46.930	44.123	1.519

ly sampled; mtCR sequence data only from 14 additional *E. newberryi* demonstrated that the Ventura group did conform to the sudden expansion model ($P = 0.73$, $\Theta_0 = 1.6$, $\tau = 1.83$; M. Dawson, K. Louie, M. Barlow, D. Jacobs, and C. Swift, unpubl. data). All six groups fitted a model of long-term stable population size worse than the model of sudden expansion ($\chi^2 > 62$, $P \ll 0.005$, for all comparisons).

In addition to its low molecular diversity, the Southern (San Diego) clade was characterized by a slow rate of molecular evolution relative to the Northern clade (relative rates test using mean, uncorrected, pairwise sequence differences: Southern/Northern = 0.010/0.028; Li and Graur 1991).

DISCUSSION

Phylogeography of Eucyclogobius newberryi

Analyses of mtDNA sequence data reveal considerable phylogeographic structure within *Eucyclogobius newberryi* (Figs. 1, 3; Table 3) attributable to at least two episodes of evolution: a relatively early divergence of Southern and Northern clades and later expansion of the Northern clade. The intraspecific phylogeny also suggests there have been different processes affecting and patterns of evolution in Northern and Southern clades—probably due to climate change, tectonism, sea-level fluctuations, coastal hydrography and geography, and natural and anthropogenic extirpations.

The timing of these processes can be estimated using a molecular clock based on cyt *b* sequence data, which offers a better gauge of divergence times than mtCR (McMillan and Palumbi 1997). Acknowledging that a molecular clock will be imprecise due to rate variation between taxa, such as that between Northern and Southern clades of *E. newberryi*, cyt *b* divergence of approximately 1–2% per million years (Krajewski and King 1996; McMillan and Palumbi 1997) would date the divergence of Northern and Southern clades of *E. newberryi* at 2–4 million years ago. Variation within the Northern clade (range = 0–2.1%; mean ± SD, 0.99 ± 0.41%) likely arose less than 1–2 million years ago. Thus, the period of intraspecific evolution of *E. newberryi* encompasses considerable tectonic activity in California (e.g., Vedder and Howell 1980; Davis et al. 1989; Sorlien 1994) and multiple episodes of climate and sea-level change (Shackleton 1987; Harland et al. 1989; Dawson 1992; Gvirtzman 1994).

Presently, *E. newberryi* is restricted to coastal estuarine and wetland habitats in California (Miller and Lea 1972; Swift et al. 1989). The modern center of its range is approximately Monterey Bay. On average, however, the distribution of *E. newberryi* almost certainly has been farther south due to the predominantly cooler climate of California during the Pleistocene (Addicott 1966; Johnson 1977a; Harland et al. 1989; Graham and Grimm 1990). Reconstructions of Late Pleistocene coastal marine provinces suggest temperate Oregonian fauna, probably including ancestral Northern *E. newberryi*, were displaced south and considerably contracted (interglacial: ~48°N to 34.5°N; glacial: ~35°N to ~34°N), while warm temperate Californian fauna, probably including ancestral Southern *E. newberryi*, were displaced and contracted less (interglacial: ~34.5°N to 28°N; glacial: ~34°N to 28°N; Addicott 1966; Fields et al. 1993). Thus,

TABLE 3. Contributions of five phylogeographic boundaries to genetic structure in *E. newberryi*. The AMOVA distance matrix constituted uncorrected sequence differences. Probabilities were calculated using 40,200 permutations of the datamatrix.

Phylogeographic boundary	All five[1]	LAR[2]	Seacliff[3]	MB-PtB[4]	BSC[5]	SC-PtA[6]
Source and % of variation						
Among regions	79.46	51.26	77.92	75.19	74.12	77.17
Among populations within regions	7.15	35.06	9.14	12.07	13.03	10.09
Within populations	13.39	13.68	12.93	12.74	12.85	12.75
Fixation indices[7]						
Φ_{CT}	0.7947*	0.5126*	0.7792*	0.7519*	0.7412*	0.7717*
Φ_{SC}	0.3481*	0.7194*	0.4142*	0.4864*	0.5036*	0.4418*
Φ_{ST}	0.8661*	0.8633*	0.8707*	0.8726*	0.8715*	0.8726*

[1] Six groups were defined according to the *E. newberryi* phylogeny: ({Cape} {SF} {PtC} {V} {EB} {SD} ≈ ((((Cape), SF ((PtC), (V))), (EB)), (SD)). The relative contributions to this hierarchical structure of five observed phylogeographic boundaries were assessed by collapsing groups as follows.

[2] LAR, Los Angeles region ({Cape} {SF} {PtC} {V} {EB SD}).

[3] Seacliff ({Cape} {SF} {PtC} {V EB} {SD}).

[4] MB-PtB, Morro Bay–Point Buchon ({Cape} {SF} {PtC EB} {V} {SD}).

[5] BSC, Big Sur coastline ({Cape} {SF EB} {PtC} {V} {SD}).

[6] SC-PtA, Salmon Creek–Point Arena, ({Cape SF} {PtC} {V} {EB} {SD}).

[7] Correlation of random haplotypes: Φ_{CT} within groups versus whole species; Φ_{SC} within populations versus regions; Φ_{ST} within populations versus whole species.

[8] Probability of an equal or more extreme Φ-statistic and associated variance component (σ) by chance alone, P, was <0.001, as determined by appropriately constrained permutations of the data matrix (Excoffier et al. 1992). All Φ and σ were significant at $P < 0.05$, as indicated by an asterisk following sequential Bonferroni adjustment for 18 tests (Rice 1989).

TABLE 4. Relative magnitudes of five phylogeographic boundaries affecting *E. newberryi*.

Phylogeographic boundary	LAR[1]	Seacliff[2]	MB-PtB[3]	BSC[4]	SC-PtA[5]
Mean genetic difference (no. of nucleotides)	45.0	5.2	11.9	13.2	4.4
Mean geographic distance (km)	215	67	50	193	131
Magnitude (genetic difference/100 km)	20.93	7.76	23.80	6.84	3.36

[1] LAR, Los Angeles region, San Diego (north) to Ventura.
[2] Seacliff, Ventura to Pt. Conception (south).
[3] Pt. Conception (north) to Estero Bay (south).
[4] Estero Bay (north) to San Francisco (south).
[5] San Francisco (north) to Cape Mendocino (south).

predominantly Oregonian, cooler-water, coastal marine fauna likely found refuge around Ventura and the northern Channel Islands (Valentine 1958; Lindberg and Lipps 1996), but possibly as far south as the Southern California Bight during some glacial maxima (see Mortyn et al. 1996), whereas the Los Angeles coastline may still have been inhabited predominantly by Californian fauna (Valentine 1958).

Accordingly, sequence and phylogenetic analyses suggest the Southern clade's ancestral range was southern California, whereas the Northern clade's ancestral range was Estero Bay and possibly San Francisco during the mid to late Pleistocene. Estero Bay and San Francisco groups have relatively high nucleotide diversity, π, and high haplotype diversity, h (Table 5), which suggest these groups have long histories with reasonably stable population sizes (Grant and Bowen 1998; Avise 2000, p. 59). The shapes of mismatch distributions and estimates of initial population sizes (Θ_0) and mutational timescales (τ) also suggest that Estero Bay and San Francisco groups have historically larger and older populations than other Northern groups (Fig. 5; Rogers and Harpending 1992). Phylogenetic analyses are consistent with this interpretation and indicate further that the Estero Bay group is basal to the San Francisco group (Fig. 3). The occurrence of derived haplotypes to both the north (San Francisco) and south (Point Conception) is geographically most parsimonious if Estero Bay was the ancestral area of the present-day Northern clade (see Cann et al. 1987; Vigilant et al. 1991).

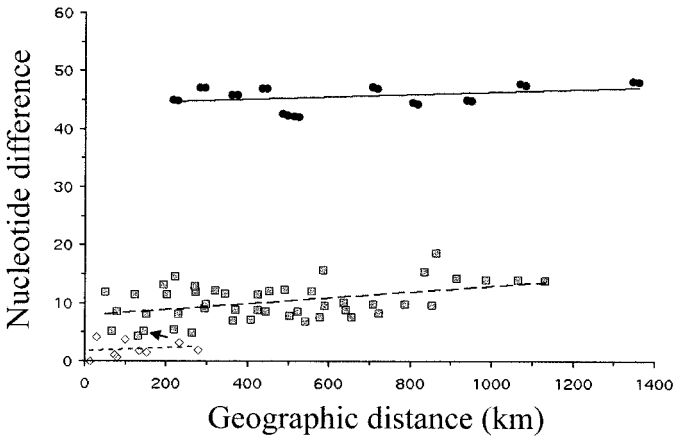

FIG. 4. Regression of mean genetic distance (mean number of nucleotide differences) on mean geographic distance (km). Except Ventura, each phylogeographic group was divided into northern and southern (Cape Mendocino, Estero Bay, and San Diego) or northern, central, and southern (San Francisco and Point Conception) members to allow three levels of comparison. First, between San Diego and all Northern groups, that is, across LAR (black circles, solid line; $y = 44.221 + 0.002x$, $R^2 = 0.138$, $P = 0.089$). Second, among Northern groups only (gray squares, dashed line; $y = 7.843 + 0.005x$, $R^2 = 0.194$, $P = 0.002$). Third, between northern, central, and southern members within each of the six recognized groups (white diamonds, dotted line; $y = 1.725 + 0.003x$, $R^2 = 0.028$, $P = 0.665$). The arrow points to the comparison of pairwise genetic and geographic distances across the biogeographic boundary at Point Conception.

At least once since the mid to late Pleistocene, therefore, the range of *E. newberryi* likely expanded from Estero Bay northward into the San Francisco region and southward into the Point Conception region. The derived status and northerly situation of the Cape Mendocino group relative to San Francisco, and the general occurrence of more derived haplotypes further north within Cape Mendocino, suggest that northward expansion was progressive and stepwise. It probably also was at times rapid, as indicated by the poorly resolved starlike phylogeny north of Estero Bay and rates of Pleistocene climate change (e.g., Dawson 1992, p. 22), and may have occurred in several waves, which is consistent with more than one mode in the mismatch distribution of the San Francisco group (Fig. 5B; Torroni et al. 1992; Harpending et al. 1993; Horai et al. 1993) and with cyclic patterns of climate change (Johnson 1977a; Graham and Grimm 1990; Stine 1990; Dawson 1992; Davis 1999). Several waves of expansion also may be apparent in the Cape Mendocino mismatch distribution (Fig. 5A), although this polymodal distribution may be influenced more (and perhaps the San Francisco distribution to some extent) by differentiation of distant populations and limited movement of individuals in this northernmost group (Figs. 1, 3; Harpending et al. 1993; Avise 2000). Currently, the northward expansion has been curtailed at the Smith River (Miller and Lea 1972; Swift et al. 1989). Similarly, the southward expansion that established the Point Conception group continued into Ventura but stopped somewhere north of, in, or near, the LAR. However, the molecular diversity and mismatch distributions of Point Conception, Ventura, San Francisco, and Cape Mendocino groups (Fig. 5; Table 5) suggest that southward expansion occurred later and under somewhat different conditions than northward expansion(s). For example, in contrast to more northerly groups, the Point Conception clade is described by a highly leptokurtic, normal distribution that fits exceedingly well the distribution expected of a single sudden population expansion, which may have resulted from reestablishment or reinvasion of the region from Estero Bay or by contraction and subsequent expansion of an already resident Point Conception font clade.

However, genetic and geographic distances among popu-

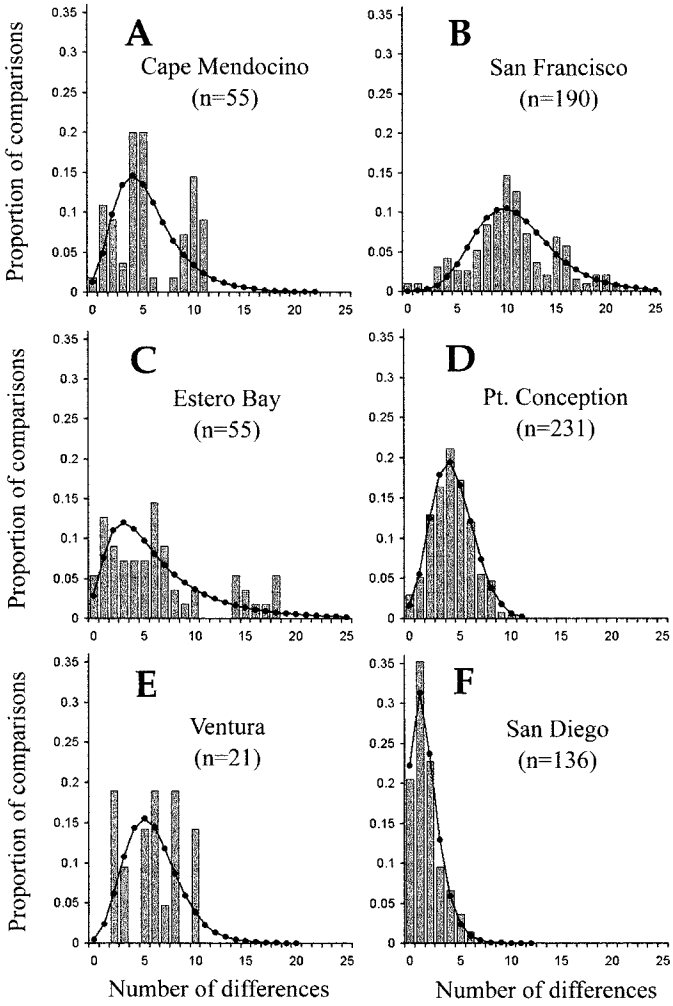

FIG. 5. Intragroup mismatch distributions. The observed distributions (bars) are compared for their goodness of fit to the sudden expansion model (GoF_{SEM}; Rogers and Harpending 1992) illustrated by the overlayed curve (black circles, solid line). (A) Cape Mendocino group: $\Theta_0 = 2.44$, $\tau = 3.13$, Harpending's raggedness index (HRI) = 0.092; goodness of fit of observed data to sudden expansion model (GoF_{SEM}), $\chi^2 = 23.1$, df = 6, $P = 0.001$. (B) San Francisco group:. $\Theta_0 = 2.64$, $\tau = 8.44$, HRI = 0.015; GoF_{SEM}, $\chi^2 = 41.2$, df = 14, $P < 0.001$. (C) Estero Bay group. $\Theta_0 = 4.57$, $\tau = 3.57$, HRI = 0.028; GoF_{SEM}, $\chi^2 = 15.8$, df = 7, $P = 0.027$. (D) Point Conception group: $\Theta_0 < 0.01$, $\tau = 4.31$, HRI = 0.02 (model fitted in Arlequin ver. 2.0); GoF_{SEM}, $\chi^2 = 6.38$, df = 9, $P > 0.5$. (E) Ventura group: $\Theta_0 = 1.29$, $\tau = 4.52$, HRI = 0.20; GoF_{SEM}, $\chi^2 = 0.33$, df = 1, $P = 0.57$. (F) San Diego group: $\Theta_0 = 0.59$, $\tau = 1.04$, HRI = 0.057; GoF_{SEM}, $\chi^2 = 2.97$, df = 4, $P = 0.56$.

lations of *E. newberryi* are weakly correlated ($R^2 = 0.251$) indicating that the present-day phylogeographic structure of the tidewater goby is not simply the result of stepping-stone gene flow driven by Pleistocene climate change. AMOVA (Table 3) and significant differences in mtDNA sequence divergence (Fig. 4) demonstrate that migration between populations within groups is easier than migration between groups. This can be explained by the occurrence of phylogeographic groups of *E. newberryi* generally within littoral cells that support the formation of closely spaced lagoons and estuaries (Swift et al. 1989) and, therefore, the occasional successful migration by even extremely poor dispersers such as *E. newberryi* during favorable conditions. Such cells may, therefore, contain metapopulations (Lafferty et al. 1999a,b). In contrast, tidewater gobies are absent and phylogeographic breaks occur where precipitous coastlines preclude suitable habitat from forming (Swift et al. 1989). Thus, the phylogenetic magnitude of some breaks (e.g., Big Sur) may largely be a function of their length, whereas others (e.g., the Morro Bay/Point Buchon break) are much stronger than would be predicted solely from their length (Table 4). These stronger breaks probably indicate additional barriers to gene flow, such as headlands, estuaries, or other features that interrupt long-shore flow, divert coastal currents offshore, and create fronts and eddies that might isolate planktonic larvae and facilitate genetic differentiation (see Owen 1980; Wolanski and Hamner 1988; Brink and Cowles 1991; Bucklin 1991; Moser and Smith 1993; Ruzzante et al. 1998).

The strongest phylogeographic break by far separates all Northern from all Southern *E. newberryi* (Figs. 3, 4; LAR, Tables 2–4). This break likely results from superposition of several barriers to gene flow on time scales of millions of years to decades including Pliocene-Pleistocene uplift of the Northern Channel Islands that annexed the Southern California Bight (Sorlien 1994; Ingersoll and Rumelhart 1999), transition of LAR from a marine to terrestrial environment (Davis et al. 1989) that reduced the habitat available to *E. newberryi* leading to extirpation of populations, and a dozen or so Pleistocene cycles of climate and sea-level change (Bloom et al. 1974; Shackleton 1987; Harland et al. 1989; Dawson 1992; Gvirtzman 1994) that involved periods of drought (Davis 1999) that may have desiccated *E. newberryi* habitat and low stands that decreased the width and depth of seaways (Johnson 1977b), thus promoting isolation of populations in the bight from those in surrounding waters. Other events, such as great floods (Schimmelmann et al. 1992, 1998), tsunami (Hauksson and Saldivar 1989), and features such as the Palos Verdes Peninsula and large (presently submarine) canyons, similarly may have affected patterns of hydrography, habitat distribution, and gene flow or extirpation in *E. newberryi.* The disjunct distribution of Southern *E. newberryi* at the species's southern limit, and the probable late Pleistocene absence (or replacement) of *E. newberryi* from Point Conception and Ventura regions (Figs. 3, 5D) suggest these environmental factors fragmented a Plio-Pleistocene, glacial, more southerly distribution of *E. newberryi* steepening an existing cline or creating a phylogeographic break across the LAR. Subsequent movement northward of the presumptive Northern clade, as well as further tectonism, climate change, and related events, likely consolidated this fragmentation. After, and probably during, its establishment, the Southern lineage experienced at least one, and maybe many, bottlenecks as evident in its present-day low genetic diversity (Fig. 5F; Table 5).

This interpretation, however, may be confounded by the extirpation of 25–50% of *E. newberryi* populations attributable to coastal development, agriculture, and other human activities that were concentrated around San Francisco Bay, Los Angeles, and San Diego during the 1900s (Swift et al. 1989; Lafferty et al. 1996; Ballard et al. 1999). Indeed, only three natural populations remained in or south of Los Angeles

TABLE 5. Molecular diversity of six phylogeographic groups in *E. newberryi*. The variables *ah* and $a\pi$ are values of *h* and π adjusted for possible PCR error. The corresponding range of standard deviations is given. The categories low and high are less than or greater than, respectively, the value 0.5 for both haplotype and nucleotide diversity, as defined by Grant and Bowen (1998). L/H, borderline low/high.

Group	Haplotype diversity (ah–h ± SD)	Nucleotide diveristy ($a\pi$–π ± SD)%
Cape Mendocino	0.927–0.964 ± 0.051–0.054 high	0.39–0.43 ± 0.24–0.25 low
San Francisco	0.968–0.990 ± 0.019–0.025 high	0.73–0.82 ± 0.39–0.44 high
Estero Bay	0.873–0.945 ± 0.066–0.089 high	0.35–0.58 ± 0.22–0.33 L/H
Pt.Conception	0.853–0.970 ± 0.024–0.048 high	0.23–0.34 ± 0.14–0.20 low
Ventura	0.952–1.000 ± 0.076–0.095 high	0.30–0.36 ± 0.20–0.23 low
San Diego	0.427–0.794 ± 0.104–0.147 L/H	0.05–0.13 ± 0.05–0.09 low

County in March 1994 (Swift et al. 1989), when *E. newberryi* was listed as a federally endangered species, and numbers have remained low since. Thus, the current lack of diversity in Southern *E. newberryi* might solely be a modern attribute—the construction of LAR within the last two centuries could, alone, have extirpated undocumented *E. newberryi* populations that were intermediate between Estero Bay and San Diego groups, resulting in a pattern similar to the one we have attributed here to tectonic, climatic, and other factors. However, the depth of the LAR break, the reestablishment (or replacement) of Point Conception and Ventura groups at least once since divergence of the Southern clade, and the relatively slow rate of molecular evolution in the Southern clade suggest that Southern *E. newberryi* do have a long history of isolation, bottlenecks, and limited geographic range (see Carson and Templeton 1984; Galiana et al. 1993; Futuyma 1998, p. 304). This distinction, between ancient natural and recent human effects, demonstrates the important role of phylogeographic studies in conservation biology (e.g., Avise 2000, pp. 268–276); a role that is emphasized by the discovery of genetically distinct groups of *E. newberryi* among Northern populations that, on the basis of ecological data alone (Lafferty et al. 1999a,b), generally have been considered well mixed in recent proposals for delisting (Ballard et al. 1999).

Comparative Phylogeography of Coastal California Taxa

In contrast to coastal maritime taxa in the southeastern United States, generally little phylogeographic structure has been found in coastal maritime taxa of the southwestern United States (see summaries in Avise 1992; Burton 1998). However, four recent studies have now found considerable phylogeographic structure in *Tigriopus californicus* (Burton 1998), *Nucella emarginata* (Marko 1998), *Embiotoca jacksoni* (Bernardi 2000), and *Eucyclogobius newberryi* (this study) off southwestern United States. Notably, these four taxa have been studied with mtDNA, have limited dispersal ability, and inhabit somewhat patchy environments—attributes they share in common with the most deeply phylogeographically structured taxa in the Southeast.

Contrary to southeastern taxa, however, the southwestern taxa studied indicate phylogeographic patterns are not concordant with biogeographic patterns at major points (Burton 1998). This is not predicted by phylogeographic theory (Avise et al. 1987) and may suggest that different processes are operating in these regions (Burton 1998). An alternative interpretation, suggested by the close concordance of three phylogeographic breaks in the Southern California Bight (Burton 1998; Bernardi 2000; this study), is that phylogeographic and biogeographic patterns are concordant and, therefore, that the principal biogeographic break is not at Point Conception but in the LAR (Dawson 2000).

Summary

The intraspecific phylogeny of the tidewater goby, an inhabitant of discrete, seasonally closed estuaries that has low dispersal ability, is highly geographically structured. Six major phylogeographic groups in four clusters—the San Diego clade south of Los Angeles, the Point Conception and Ventura groups between Los Angeles and Point Buchon, a lone Estero Bay group from central California, and San Francisco and Cape Mendocino groups from northern California—are distinguished by haplotype and nucleotide variation and likely barriers to gene flow in the vicinities of Los Angeles, Seacliff, Point Buchon, Big Sur, and Point Arena. Finer-scale phylogeographic structure within these regions is suggested by haplotype and nucleotide differences between estuaries, but is poorly resolved by current analyses.

The phylogenetic relationships between and patterns of molecular diversity within the six groups are consistent with repeated and sometimes rapid northward and southward range expansions out of central California, likely caused by Quaternary climate change. In addition, the modern geographic and genetic structure of *E. newberryi* probably also has been influenced by patterns of expansion and contraction, colonization, extirpation, and gene flow linked to Pliocene-Pleistocene tectonism, Quaternary coastal geography and hydrography, and historical human activities.

Notably, the deepest phylogenetic gap in *E. newberryi* coincides with phylogeographic breaks in several other coastal California taxa in the vicinity of Los Angeles, suggesting common extrinsic factors have had similar effects on different species in this region. In contrast, there is evidence in this species of gene flow across the biogeographic boundary at Point Conception.

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